A New Genus of Pennsylvanian Fish (Crossopterygii, Coelacanthiformes) from Kansas

BY

JOAN ECHOLS

University of Kansas
Lawrence, Kansas

A New Genus of Pennsylvanian Fish (Crossopterygii, Coelacanthiformes) from Kansas

BY

JOAN ECHOLS

INTRODUCTION

In 1931 and 1932, H. H. Lane, C. W. Hibbard and W. K. Mc-Nown collected the specimens that Hibbard (1933) described and made the basis of two new species. These were from the Rock Lake shale member of the Stanton formation, six miles northwest of Garnett, Anderson County, Kansas. In 1954, from a locality (KAn-1/D, see page 480) approximately one fourth mile southwest of the first locality, specimens were quarried by F. E. Peabody, R. W. Wilson and R. Weeks. In 1955 R. R. Camp collected additional blocks of Rock Lake shale from this second locality. Study of all of the materials from the above mentioned localities reveals the existence of an hitherto unrecognized genus of coelacanth. It is named and described below.

SYSTEMATIC DESCRIPTIONS
Subclass CROSSOPTERYGII
Superorder COELACANTHI
Order Coelacanthiformes
Suborder DIPLOCERCIDOIDEI
Family DIPLOCERCIDAE

Subfamily Rhabdodermatinae, new subfamily

Type genus.—*Rhabdoderma* Reis, 1888, Paleontographica, vol. 35, p. 71.

Referred genus.—*Synaptotylus* new, described below.

Horizon.—Carboniferous.

Diagnosis.—Sphenethmoid region partly ossified, and consisting of basi-sphenoid, parasphenoid, and ethmoid ossifications; paired basipterygoid process and paired antotic process on basisphenoid; parasphenoid of normal size, and closely associated with, or fused to, basisphenoid; ethmoids paired in *Rhabdoderma* (unknown in *Synaptotylus*).

Discussion.—Because of the great differences in endocranial structure between the Devonian and Pennsylvanian coelacanths, they are here placed in new subfamilies. The two proposed sub-families of the family Diplocercidae are the Diplocercinae and the Rhabdodermatinae. The Diplocercinae include those coelacanths having two large unpaired bones in the endocranium (at present this includes *Diplocercides* Stensiö, *Nesides* Stensiö and *Euporosteus* Jaekel). The subfamily Rhabdodermatinae is composed of coelacanths having reduced endocranial ossification, as described in detail above, and now including *Rhabdoderma* Reis and *Synaptotylus* n. g.

Members of this subfamily differ from those of the subfamily Diplocercinae in having several paired and unpaired elements in the sphenethmoid region of the endocranium, instead of only one larger ossification. They differ from those of the suborder Coela-canthoidei in the retention of basipterygoid processes.

Synaptotylus is more closely related to *Rhabdoderma* than to the Diplocercines because the anterior portion of the endocranium contains only a basisphenoid, parasphenoid, and probably ethmoids. The sphenethmoid region was certainly not a large, unpaired unit as in the Diplocercines. Probably the posterior part, the otico-occipital region (not known in *Synaptotylus*), was much more nearly like that of *Rhabdoderma,* which consisted of unpaired basi-occipital and supraoccipital, and paired prootics, exoccipitals, and anterior and posterior occipital ossifications (Moy-Thomas, 1937:

figs. 3, 4). Moy-Thomas (1937:389) points out that in *Rhabdo-*
derma the occipital region is "considerably more ossified" than in
any coelacanths other than the Devonian forms. Berg (1940:390)
thought that the Carboniferous coelacanths should be placed in a
separate family because they did not have two large, unpaired
bones in the endocranium. *Rhabdoderma* and *Synaptotylus* repre-
sent another stage in evolution of the endocranium in coelacanths,
and, if classification is to be based on endocranial structure, then
this stage (represented by the two genera) may later be given
family rank as Berg suggested. Because *Rhabdoderma* and *Synap-*
totylus have only part of the sphenethmoid region ossified and be-
cause they retain basipterygoid processes, they are considered to be
related and are included in the subfamily Rhabdodermatinae.

Synaptotylus, new genus

Type species.—*Synaptotylus newelli* (Hibbard).

Horizon.—Rock Lake shale member, Stanton formation, Lansing group,
Missouri series, Upper Pennsylvanian.

Diagnosis.—Late Pennsylvanian fishes of small size, having the
following combination of characters: on basisphenoid, knoblike
antotic processes connected by a low ridge to basipterygoid proc-
esses; entire ventral surface of parasphenoid toothed; anterior mar-
gin of parasphenoid notched and no evidence of hypophyseal
opening. Dermal bones of skull smooth or with low, rounded
tubercles and striae; fronto-ethmoid shield incompletely known
but having one pair of large rectangular frontals with postero-
laterally slanting anterior margins; intertemporals large, the lateral
margins curving laterally; postorbital triangular, apex downward;
subopercular somewhat triangular; squamosal carrying sensory
canal that curves down posteriorly and extends onto a ventral pro-
jection; opercular generally triangular; supratemporals elongate,
curving to fit lateral margin of intertemporals; circumorbital plates
lightly ossified. Palatoquadrate complex consisting of endoptery-
goid and ectopterygoid (both toothed on medial surface), quadrate,
and metapterygoid, the latter smooth and having widened border
for articulation on anterodorsal margin. Pectoral girdle consisting
of cleithrum and clavicle (supracleithrum not seen); small projec-
tion on medial surface of posterior portion of cleithrum; horizontal
medial process on clavicle. Pelvic plate bearing three anteriorly
diverging apophyses, and one denticulate ventromedian process
for articulation to opposite plate. Lepidotrichia jointed distally,

but not tuberculated. Scales oval, having posteriorly converging ridges on posterior exposed parts.

The name refers to the most distinctive character of the genus, the connected antotic and basipterygoid processes on the basisphenoid, and is derived from Greek, *synaptos*—joined, *tylos* (masc.)—knob, projection.

Synaptotylus is excluded from the advanced suborder Coelacanthoidei by the retention of basipterygoid processes on the basisphenoid. *Synaptotylus* differs from *Rhabdoderma* in several characters of the basisphenoid, the most important being: knoblike antotic processes (those of *Rhabdoderma* are wider, more flattened and more dorsal in position); small, lateral basipterygoid processes (in *Rhabdoderma* these are larger and farther ventral in position).

Synaptotylus newelli (Hibbard)

Coelacanthus newelli Hibbard, 1933, Univ. Kansas Sci. Bull., 21:280, pl. 27, figs. 2, 3.

Coelacanthus arcuatus Hibbard, 1933, Univ. Kansas Sci. Bull., 21:282, pl. 26, fig. 8; pl. 27, fig. 1.

Rhabdoderma elegans Moy-Thomas, 1937 (in part), Proc. Zool. Soc. London, 107(ser. B, pt. 3):399.

Type.—K. U. no. 786F.

Diagnosis.—Same as for the genus.

Horizon.—Rock Lake shale member, Stanton formation, Lansing group, Missouri series, Upper Pennsylvanian.

Localities.—The specimens studied by Hibbard (K. U. nos. 786F, 787F, 788) and no. 11457 were taken from the Bradford Chandler farm, from the original quarry in SW¼, SE¼, sec. 32, T.19S, R.19E. The remainder were collected from University of Kansas Museum of Natural History locality KAn-1/D, a quarry in sec. 5, T.19S, R.19E. Both of these are approximately six miles northwest of Garnett, Anderson County, Kansas.

Referred specimens.—K. U. nos. 786F, 787F, 788, 9939, 11424, 11425, 11426, 11427, 11428, 11429, 11430, 11431, 11432, 11433, 11434, 11449, 11450, 11451, 11452, 11453, 11454, 11455, 11457.

Preservation.—Preservation of many of the specimens is good, few are weathered, but most of the remains are fragmentary and dissociated. One specimen (the type, no. 786F) and half of another were nearly complete. Specimens are found scattered throughout the Rock Lake shale (see p. 498).

Morphology.—Terminology used for bones of the skull is that of Moy-Thomas (1937) and Schaeffer (1952).

Endocranium and parasphenoid

The basisphenoid (see fig. 1) has been observed in only one specimen (K. U. no. 9939) in posterodorsal and ventral views. The basisphenoid, although somewhat crushed, appears to be fused to the parasphenoid. Both antotic and basipterygoid processes are
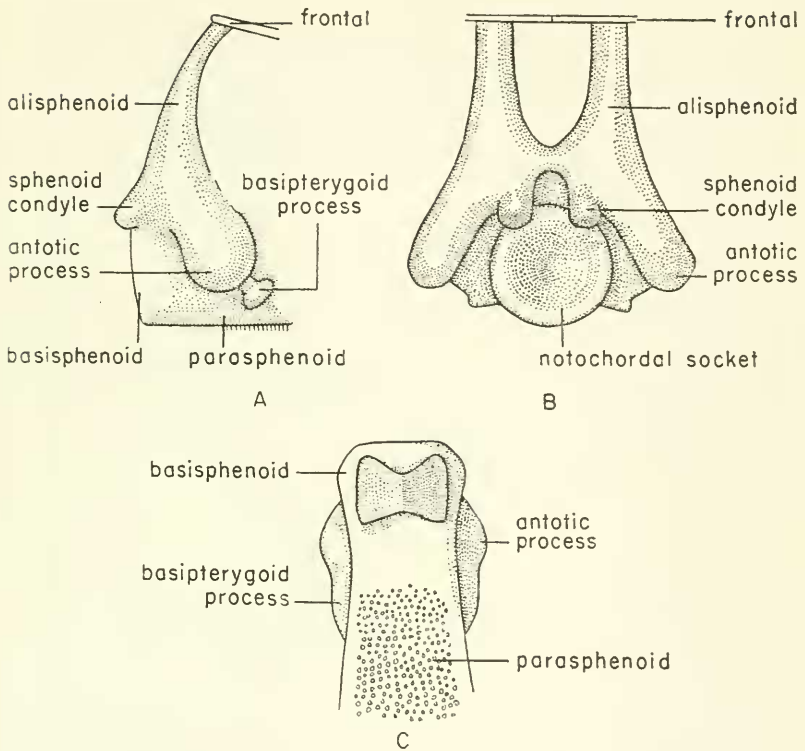
Fig. 1. *Synaptotylus newelli* (Hibbard). Restoration of the basisphenoid, based on K. U. no. 9939, × 5. A, lateral view, B, posterior view, C, ventral view.

present, and are connected by a low, rounded ridge. The antotic processes are large, bulbar projections. These processes in *Rhabdoderma* are wider and more flattened (Moy-Thomas, 1937:figs. 3, 4). The antotic processes are at mid-point on the lateral surface, not dorsal as in *Rhabdoderma*, and both the processes and the ridge are directed anteroventrally. The basipterygoid processes are smaller, somewhat vertically elongated projections, situated at the end of the low connecting ridge extending anteroventrally from the antotic processes, and are not basal as are those of *Rhabdoderma*. The sphenoid condyles, seen in posterior view, issue from the dorsal margin of the notochordal socket. The margins of the socket are rounded, and slope down evenly to the center. A slight depression situated between and dorsal to the sphenoid condyles is supposedly for the attachment of the intercranial ligament (Schaeffer and Gregory, 1961:fig. 1). The alisphenoids extend

upward, anterodorsally from the region above the sphenoid condyles, and may connect to ridges on the ventral surface of the frontals. The lateral laminae are not preserved, and their extent is unknown.

In viewing the changes in the endocranium of Carboniferous and Permian coelacanths, it would be well to consider the mechanical relationship of the loss of the basipterygoid processes to the effect on swallowing prey. Evidently many of the coelacanths, *Latimeria* for example, are predators (Smith, 1939:104); to such fishes a more efficient catching and swallowing mechanism would be an adaptive improvement. Stensiö (1932:fig. 14) presents a cross section of the ethmosphenoid moiety of the endocranium of *Diplocercides kayseri* (von Koenen) showing the metapterygoid of the palatoquadrate loosely articulated to both the antotic and basipterygoid processes. According to Tchernavin (1948:137) and Schaeffer and Rosen (1961:190) the swallowing of large prey depends on the ability of the fish to expand its oral cavity by allowing the posteroventral portion of the palatoquadrate and the posterior end of the mandible to swing outward. Where the palatoquadrate articulates with the basisphenoid at the antotic and basipterygoid processes, as in the Devonian coelacanths, it can not swing so far laterally as where it articulates with only the dorsal, antotic process. Perhaps the loss of the basipterygoid articulation reflects the development of a more efficient mechanism for swallowing prey in these fishes. Schaeffer and Rosen (1961:191, 193) show that in the evolution of the actinopterygians several changes improved the feeding mechanism: some of these changes are: (1) freeing of the maxilla from the cheek, giving a larger chamber for the action of the adductor mandibulae; (2) development of a coronoid process on the mandible; and (3) increase in torque around the jaw articulation. In coelacanths, at least some comparable changes occurred, such as: (1) loss of the maxillary, thus increasing the size of the adductor chamber; (2) development of the coronoid bone, affording a greater area for muscle attachment; (3) development of an arched dorsal margin on the angular; (4) modification of the palatoquadrate complex, with resultant loss of the basipterygoid processes. In *Synaptotylus* the basipterygoid processes are small, not basally located, and perhaps not functional. A more efficient feeding mechanism developed rapidly during the Carboniferous and has remained almost unaltered.
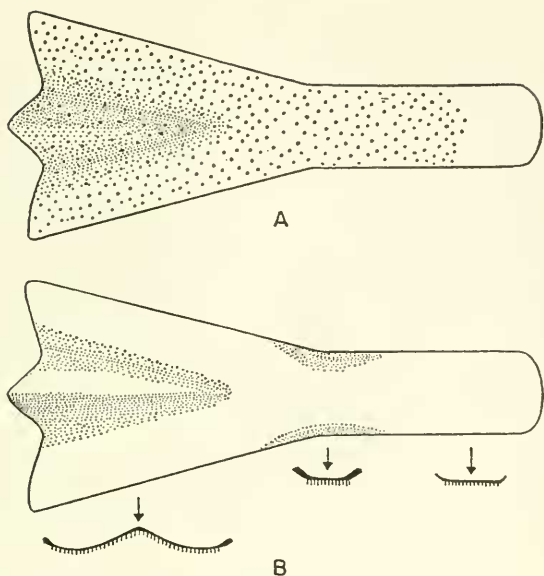
Fig. 2. *Synaptotylus newelli* (Hibbard). Restoration of the parasphenoid, based on K. U. nos. 9939, 11451, × 5.   A, ventral view, B, dorsal view and cross sections.

The parasphenoid (see fig. 2) is a shovel-shaped bone having a wide anterior portion and a narrower posterior portion of nearly uniform width.   Most of the ventral surface is covered with minute granular teeth.   The anterior margin is flared and curved postero-medially from the lateral margin to a median triangular projection. The lateral margins curve smoothly from the greatest anterior width to the narrow central portion, where the margins become somewhat thickened and turned dorsally.   Posterior to this the lateral margins are probably nearly straight.   The external surface of the anterior section is nearly flat and has a central depressed area the sides of which slope evenly to the center.   The internal surface is smooth and centrally convex.   Because of the fragmentary nature of all four observed specimens, total length was not measured but is estimated to be 15 to 20 mm.   The opening of the hypophyseal canal was not present, possibly because of crushing.   Ethmoidal ossifications were not preserved in any of the specimens studied. The parasphenoid differs from that of *Rhabdoderma elegans* (Newberry) in being more flared and widened anteriorly and more concave centrally.

Dermal bones of the skull

Various portions of the cranial roof are preserved in several specimens (see fig. 3). For comparisons with *Rhabdoderma elegans*, see Moy-Thomas (1937:fig. 1).

The premaxillaries and rostral elements are not preserved in any of the specimens. Only one pair of relatively large frontals have been observed; they are 5.5 to 9.0 mm. long and 2.0 to 3.5 mm. wide. These are nearly flat bones, with the greatest width posteriorly 0.1 to 1.0 mm. wider than the anterior portion. The midline suture is straight, the lateral margins are nearly straight, the anterior margin slopes evenly posterolaterally, and the posterior margin is slightly convex to straight. The anterior margin in *R. elegans* is essentially straight. Ornamentation consists of sparse, unevenly spaced, coarse tubercles or short striae. In one specimen both bones have small clusters of tubercles near the lateral margins and about 2.0 mm. from the posterior margin. None of these bones has alisphenoids or ridges on the ventral surface, as Stensiö (1921:65, 97) described for *Wimania* and *Axelia*.

Only six supraorbitals have been preserved (see fig. 3). These are nearly square, flat, thin bones lying nearly in place adjacent to
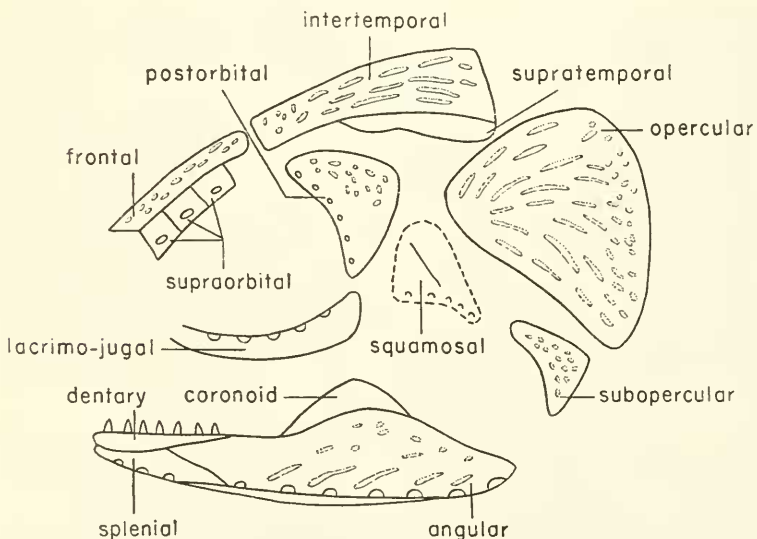

Fig. 3. *Synaptotylus newelli* (Hibbard). Diagram of the dermal bones of the skull, in lateral view, based on K. U. nos. 788 and 11432. × 2½ approximately.

a frontal on K. U. no. 788. The smallest is anterior; the margins of all are nearly straight. The bones are unornamented. Each bears a pore of the supraorbital line just below the midline. The supraorbitals of R. *elegans* have a triangular outline and do not bear pores.

Intertemporals (fig. 3) on several specimens vary from approximately 9.0 to 15.0 mm. in length, 2.0 to 2.7 mm. in anterior width, and increase to 4.5 to 8.0 mm. in maximum posterior width. The midline suture is straight, the anterior margin is concave and the lateral margin proceeds laterally in a concave curve to the widest portion. In R. *elegans* only the anterior half of the corresponding margin is concave. The posterior margin is slightly rounded and slopes anteriorly toward the lateral margin. Ornamentation is usually of randomly oriented tubercles and striae, although striae are more common in the posterior third and may be longitudinal, whereas tubercles occur mainly on the anterior section. No evidence of sensory pores, as seen on the intertemporal of R. *elegans,* has been found.

The supratemporals were observed on only one specimen (K. U. no. 788), (fig. 3). Sutures were difficult to distinguish but the medial margin is presumed to curve to fit and to articulate with the lateral margins of the intertemporals. Lateral margins are smoothly curved but the anterior and posterior margins were broken off. There appears to be no ornamentation on this bone. The supratemporals are much more elongated and curving than those in R. *elegans.*

The cheek region is nearly complete in one specimen (K. U. no. 788), and scattered parts occur in a few others (see fig. 3). The lacrimojugal of no. 788 is elongate, with both ends curving dorsally. It differs from the lacrimojugal in R. *elegans,* in which the anterior end extends anteriorly and is not curved dorsally. The posterior and anterior margins are not preserved; the greatest height appears to be posterior. Pores of the suborbital portion of the infraorbital sensory canal are seen on the dorsal surface of the bone. In R. *elegans* the pores are on the lateral surface. A section of the lacrimojugal on specimen no. 11425, broken at both ends, shows a thin layer of bone perforated by the pores and covering a groove for the canal within the dorsal margin of the bone. Both specimens are unornamented.

A nearly complete postorbital (fig. 3) on specimen no. 788 is nearly triangular, with the apex ventral. The concave anterior

margin bears pores of the postorbital part of the infraorbital line. Ornamentation consists of widely spaced, coarse tubercles.

Part of one squamosal is preserved. It is somewhat triangular and its apex is ventral. This bone is associated with the postorbital, subopercular and lacrimojugal on no. 788. The preopercular sensory line passes down the curving ventral margin of this bone, and extends ventrally onto a narrow projection. A low ridge, nearly vertical, passes dorsally from about midpoint of the canal to the dorsal portion. The anterior margin is nearly straight, the ventral margin is concave, and the dorsal margin is convex dorsally but may be incomplete. Perhaps the squamosal and preopercular are fused. The surface appears smooth; the view may be of the medial side. The squamosal of *R. elegans* is nearly triangular and notably different from that of *Synaptotylus newelli*.

The subopercular (fig. 3) shows closely spaced tubercles on the lateral surface. The bone is an elongated, irregular triangle with the apex pointing anterodorsally. The margins are incomplete, except for the concave, curving anterior margin.

Numerous operculars (fig. 3) occur in the suite of specimens, both isolated and nearly in place. Each is subtriangular; the apex of the triangle is ventral. A slight convexity projects from the anterodorsal border. The posterior margin is broadly but shallowly indented. Otherwise the margins are smooth. Maximum height ranges from 8.0 to 11.0 mm., and maximum width from 8.0 to 13.0 mm. Ornamentation varies from a few widely spaced, randomly oriented tubercles to closely spaced tubercles merging posteriorly into striae. On some specimens these are parallel to the dorsal border, and oblique in the central portion. On the posterior margins of several operculars the striae break up into tubercles. A few operculars have closely spaced tubercles over much of the surface. The internal surface is smooth.

Visceral skeleton

The palatoquadrate complex, best seen on K. U. no. 9939 (fig. 4), consists of endopterygoid, ectopterygoid, metapterygoid and quadrate. No trace of epipterygoids, dermopalatines or autopalatines, such as Moy-Thomas (1937:392, fig. 5) described for *Rhabdoderma*, has been observed.

The endopterygoid has a long, ventral, anteriorly-directed process, and an anterodorsal process that meets the metapterygoid in forming the processus ascendens. The suture between the endoptery-
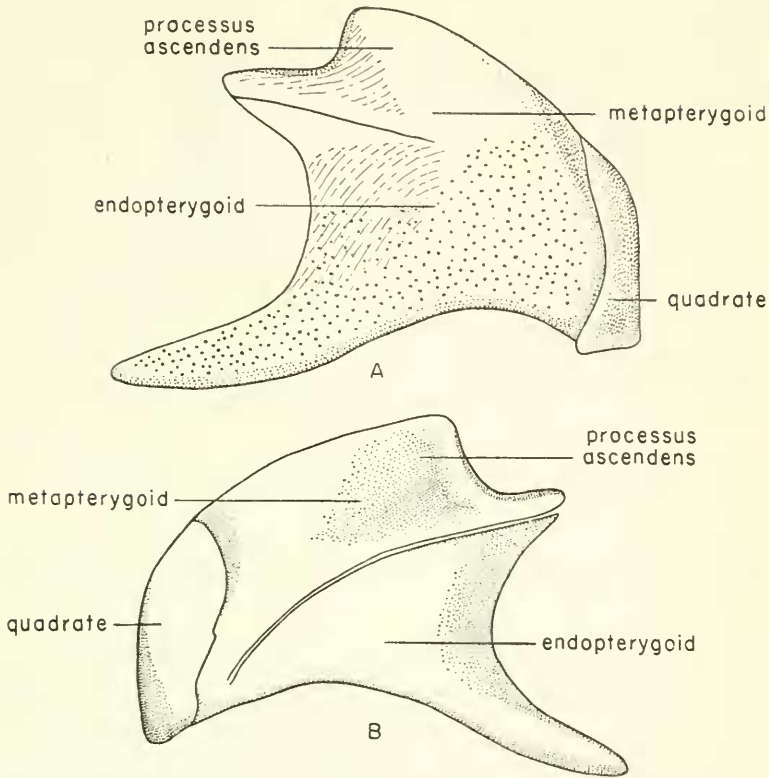
Fig. 4. *Synaptotylus newelli* (Hibbard). Restoration of the palatoquadrate complex, based on K. U. no. 9939, × 5. A, medial view, B, lateral view.

goid and metapterygoid, seen in lateral view, is distinct in some specimens and has an associated ridge; these bones appear to be fused in others, without regard to size. This suture curves dorsally from a point anterior to the quadrate and passes anterodorsally to the extremity of the processus ascendens. The suture is visible on the medial side only near the processus ascendens, for it is covered by a dorsal, toothed extension of the endopterygoid. The endopterygoid has a smooth lateral surface; the medial surface is covered with tiny granular teeth, in characteristic "line and dot" arrangement. The teeth extend onto the ventral surface of the ventral process.

Two long, narrow, splintlike bones covered on one surface with granular teeth are interpreted as ectopterygoids. These are 13.0 and 16.0 mm. long and each is 1.5 mm. wide. Orientation of these is unknown, but they probably fitted against the ventral surface
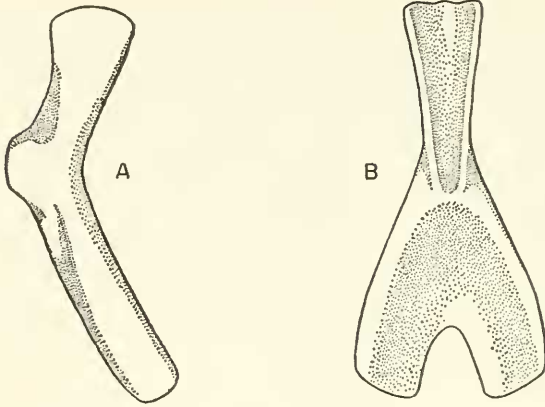
Fig. 5. *Synaptotylus newelli* (Hibbard). A, cerato-
hyal, lateral (?) view, based on K. U. nos. 11429 and
11457, × 5.   B, urohyal, based on K. U. no. 11457,
× 5.

of the ventral process of the endopterygoid (Moy-Thomas, 1937:
fig. 5).

The metapterygoid has a smooth surface in both views.   The
dorsal edge has a thickened, flared margin that presumably articu-
lated with the antotic process of the basisphenoid.   No articular
surface for the basipterygoid process has been observed.

The quadrate is distinct and closely applied to the posteroventral
margin of the complex.   In medial view the margin is nearly straight
and continues to the ventral edge.   The ventral surface is thick-
ened and forms a rounded, knoblike articular surface.   In lateral
view the surface is smooth; the anterior margin is irregular (or
perhaps broken on all specimens), and proceeds in an irregular
convex curve from the posterior to the ventral margin.

The general shape of the palatoquadrate complex is most nearly
like that of *Rhabdoderma elegans* (Moy-Thomas, 1937:fig. 5).
The orientation of the complex in the living fish was probably
oblique, with the processus ascendens nearly vertical, the quadrate
oblique, and the ventral process of the endopterygoid extending
dorsoanteriorly and articulating with the parasphenoid.

Of the hyoid arch only the ceratohyals (see fig. 5A) are preserved
in several specimens.   These are long, curved bones with a postero-
ventral process and widened, flaring posterior margin.   The medial
(?) surface is concave in one specimen.   The lateral (?) surface
displays a distinct ridge on several specimens, arising on the dorsal

surface opposite the posteroventral process and extending diagonally to the anteroventral end of the anterior limb. The impression of one other specimen appears to have a central ridge because of greater dorsal thickness and narrowness. Both surfaces are unornamented.

The urohyal (see fig. 5B) is an unornamented, Y-shaped bone, with the stem of the Y pointing anteriorly. Orientation with respect to dorsal and ventral surfaces is uncertain. In one view a faint ridge, also Y-shaped, occurs on the expanded posterior portion, and the surface is convex. The anterior process has a convex surface, sloping evenly off to the lateral margin; the opposite side of the process has a concave surface. The posterior portion has a slightly depressed area (see fig. 5B) at the junction of the "arms" of the Y.

The five branchial arches are represented by the ceratobranchials, several of which are preserved on K. U. no. 11431. These are long bones with anteriorly curving ventral ends. The medial surfaces are partly covered with minute granular teeth; only the dorsal part is without teeth. The dorsal articular surface is convex dorsally and rounded.

The mandible (fig. 3), the best specimens of which are K. U. nos. 788 and 11425, is seen only in lateral and ventral views, with only angular, splenial and dentary visible.

The angular forms the main body of the mandible, and is similar to that of *Spermatodus*. The dorsal margin of the angular is expanded in the central region, with some variation. One specimen has an expanded portion slightly anterior to that of the opposite angular. The articular surface near the posterior end has not been observed; the posterior end of the angular slopes off abruptly. The anterior sutures are seen in only two specimens, K. U. nos. 788, 11425. The dentary meets the angular in a long oblique suture; the dentary gradually tapers posterodorsally and ends on the dorsal surface of the angular. The splenial fits into a posteriorly directed, deep V-shaped notch on the ventral surface. The lateroventral surface of the angular contains sensory pores of the mandibular line. The ventral surface extends medially into a narrow shelf, approximately 1.0 mm. wide, which extends the full length of the bone; the external surface of this shelf is smooth and slightly concave dorsally. Ornamentation of the angular consists of tubercles and longitudinal or oblique striae, occurring mostly on the expanded portion. The medial surface is not seen. Several broken

specimens show a central canal filled with a rod of calcite; in one of these the sensory pores are also calcite-filled and appear to be connected to the rod. Thus the pores originally opened into a central canal.

The dentary is an unornamented bone with the anterior half curving medially; the greatest height is anterior. This bone in specimen K. U. no. 11425 bears irregularly spaced, simple, recurved, conical teeth; nine were counted, but there is space for many others. One other specimen, no. 11429, seems to have tiny tubercles on the surface. The dentary meets the splenial dorsally in a straight suture.

The splenial also curves medially, and as stated, meets the dentary in a straight suture. Ornamentation on this bone was not observed. The posterior margin is V-shaped and fits the notch in the angular. The ventral surface bears three or more sensory pores of the mandibular line.

The gular plates are oval. The medial margin is straight to slightly curved, the lateral margin curved crescentically, the posterior end is blunt, and the anterior end somewhat rounded. Ornamentation varies greatly; some bones show only a few tubercles, whereas others exhibit an almost concentric pattern of closely spaced striae. Typically there are some tubercles in the anterior quarter or third of the total length; these pass into longitudinally oriented striae in the posterior section. A few have only randomly oriented, widely-spaced striae. The internal surface is smooth.

The coronoid (K. U. no. 11428) is a triangular bone, with the apex pointing dorsally. The lateral surface is smooth; no teeth were observed. Moy-Thomas (1937:292, 293) mentions several tooth-bearing coronoids in *Rhabdoderma*, but as yet these have not been seen in *Synaptotylus*.

Axial skeleton

Only three specimens (K. U. nos. 786F, 787F, 11450) show parts of the vertebral column, but isolated neural and haemal arches are numerous. All are of the coelacanth type, having Y-shaped neural and haemal arches, without centra. A total count of 38 was obtained, but this was incomplete; the actual number was probably near 50. Counts of 10 and 16 haemal arches were obtained in two of the specimens. Total height of neural arches ranges from 7.5 to 12.0 mm., and of haemal arches, from 9.0 to 12.0 mm. The shorter arches are anterior and the height increases gradually to a maximum in the caudal region. Height of the spines varies from

4.0 to 9.0 mm., or from twice the height of the arch in the anterior to three times the height in the caudal region.   Total width of the base, measured in isolated specimens because lateral views in other specimens prevented measuring width, ranges from 0.7 to 4.2 mm. The short, broad arches having short spines occur at the anterior end of the spinal column; the narrower arches having tall spines occur toward the caudal end.   Broken neural and haemal arches show a thin covering of bone with a central, calcite-filled cavity, which in life may have been filled with cartilage (Stensiö, 1932:58, fig. 20).

No ossified ribs have been observed, either isolated or in place.

For further description of the axial skeleton, see Hibbard (1933).

Girdles and paired fins

A nearly complete pectoral girdle on specimen K. U. no. 11433 (see fig. 6A) has only a cleithrum and clavicle.   No evidence of an extracleithrum or supracleithrum has been observed, but the extra-cleithrum may be fused to the cleithrum.   The two bones form a boot-shaped unit, with the anteroventral part turned medially to form a horizontal process which meets the opposite half of the girdle.   In lateral view the surface is unornamented, and convex in the ventral half.   The suture between the cleithrum and clavicle begins on the expanded posterior portion, the "boot-heel," at a point immediately below the greatest width on the posterior margin,
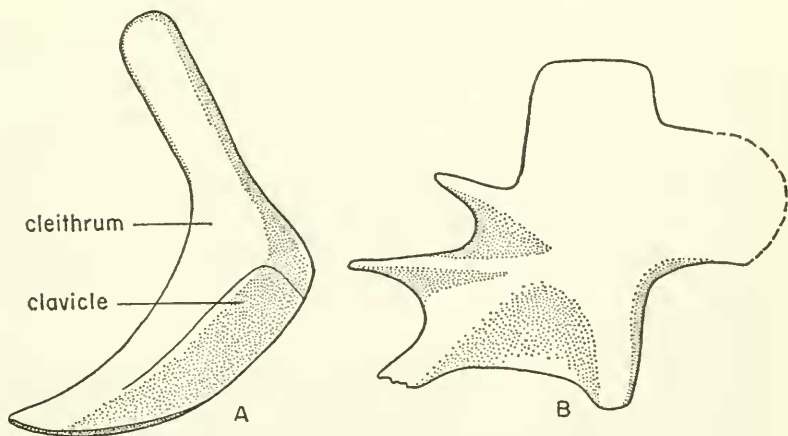

Fig. 6.   *Synaptotylus newelli* (Hibbard).   Paired fin girdles.   A, pectoral girdle, lateral view, based on K. U. no. 11433, × 3.5.   B, pelvic girdle basal plate, medial (?) view, based on K. U. no. 788, × 8.   Anterior is toward the left.

passes anteriorly, then turns sharply and parallels the anterior margin. The shape of the cleithrum resembles that in *Rhabdo- derma* and the internal surface is not ridged (see Moy-Thomas, 1937:fig. 9). The exact orientation in the fish is uncertain, but if the median extension is really horizontal, then the posterior ex- pansion is directed caudally. The medial surface is concave, steep- est near the anterior margin, and then slopes outward evenly. In medial view one specimen (K. U. no. 11426) shows a small, cau- dally directed projection of bone, evidently for articulation of the fin-skeleton, at the widest portion of the cleithrum. Sutures on several specimens were indistinct. Broken specimens show sutural faces, but many nearly complete specimens show little or no indica- tion of sutures, without regard to size of the girdles. The internal structure of the fin was not observed.

Numerous isolated basal plates of the pelvic girdle have revealed details of structure but no information on the orientation. Pre- sumably the basal plates of *Synaptotylus* had essentially the same orientation as those of other coelacanths (Moy-Thomas, 1937:395). The most complete basal plate is K. U. no. 788 (see fig. 6B). The three apophyses diverge anteriorly; the horizontal one is best de- veloped and the dorsal one is least well developed. A median process (Schaeffer, 1952:49), denticulate on several specimens, articulates with the corresponding process of the opposite plate. The expanded part that articulates with the skeleton of the fin extends caudally. The posterior expanded part is nearly square in outline, resembling the dorsal, rectangular projection. One side bears ridges leading to the extremities of the apophyses, and faint crenulations on the median process. This may be the medial view. The other view displays a smooth surface, usually without indica- tion of the ridges seen in the reverse view. These specimens differ somewhat from the basal plates of *Rhabdoderma* and appear to be intermediate between *Rhabdoderma* and *Coelacanthus* (Moy- Thomas, 1937:fig. 10A, B). The apophyses are not free as in *Rhabdoderma* but webbed with bone almost to their extremities, as in *Coelacanthus.*

The pelvic fin is seen in only two specimens (K. U. nos. 786F, 788). That on no. 788 is lobate and has 25 lepidotrichia, jointed for approximately the distal half, and 2.5 to 13.0 mm. in length. Total length of the fin is 25.0 mm. There is no trace of the internal skeletal structure or of the articulation to the basal plate in either specimen. For a description of the fin on no. 786F, see Hibbard (1933:281).

Unpaired fins

A few isolated bones on K. U. no. 788 (fig. 7) are interpreted as basal plates of the unpaired fins. For additional description of the unpaired fins on the type, K. U. no. 786F, see Hibbard (1933).

Two of these bones are flat, smooth and oblong, bearing a diagonal ridge that extends in the form of a projection. Orientation is completely unknown. These may be basal plates of the anterior dorsal fin. The fin on no. 786F that Hibbard (1933:281) interpreted as the posterior dorsal fin is now thought to be the anterior dorsal fin.
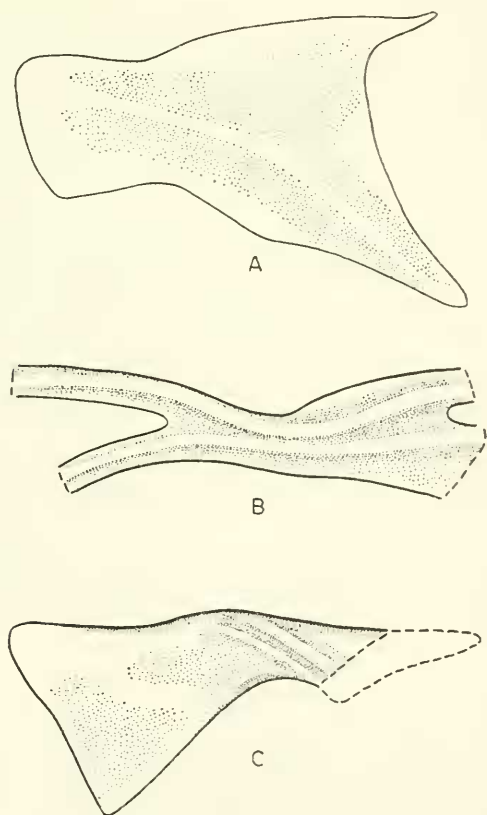

FIG. 7. *Synaptotylus newelli* (Hibbard). Basal plates of unpaired fins. A, anterior dorsal fin, based on K. U. no. 788, × 10. B, posterior dorsal fin, based on K. U. no. 788, × 12. C, anal fin, based on K. U. no. 11450, × 5. Anterior is toward the left.

One distinctive bone may represent the basal plate of the pos-
terior dorsal fin. This incomplete specimen shows two projecting
curved processes, bearing low but distinct ridges, which diverge,
probably anteriorly. The central portion is narrow. The two
ridges continue onto the posterior portion. This has been broken
off, but shows that the ridges diverge again. The surface is smooth,
except for the ridges. As before, orientation is uncertain. On no.
786F this fin was interpreted by Hibbard (1933:281) as the anal
fin.

Only part of one basal plate of the anal fin was preserved
on K. U. no. 11450. That plate is oblong and has an expanded
anterior end. The narrow, constricted part bears two oblique
ridges and a few tubercles. The posterior part has nearly straight
margins (represented by impressions) and the posterior margin
is oblique, sloping anteroventrally. The flared anterior part has
a smooth surface. This basal plate is more nearly like those of
Coelacanthus, according to the descriptions given by Moy-Thomas
(1937:399). The basal plate is associated with seven apparently
unjointed, incomplete lepidotrichia. The anal fin on no. 786F is
interpreted as the anterior dorsal fin (Hibbard, 1933:281).

The caudal fins are preserved on K. U. nos. 786F, 787F, and have
a total of 24 lepidotrichia, 12 above and 12 below. These are
jointed for the distal half or two-thirds, and are up to 16.0 mm.
in length. In specimen no. 787F the supplementary caudal fin
has at least seven lepidotrichia, the longest of which is 11.0 mm.
but incomplete. Anterior lepidotrichia appear unjointed but the
posterior ones are jointed for the distal two-thirds (?) (these are
broken off). The supplementary caudal fin is approximately 1.5
mm. long and 8.0 mm. or more wide. The supplementary caudal
fin on K. U. no. 786F described by Hibbard (1933:281) could
not be observed; this part of the caudal fin is missing.

Squamation

In the suite of specimens isolated scales are numerous, but patches
of scales are rare. Only two specimens (K. U. nos. 786F, 787F) are
complete enough for scale counts, but preservation permits only
partial counts. In general the scales resemble those of *Rhabdo-
derma elegans* (Newberry).

The scales are oval. The exposed posterior part of each bears
posteriorly converging ridges; the anterior part is widest and shows
a fine fibrillar structure. There are at least six scale-rows on either

side of the lateral line. Lateral line scales show no pores, and except for slight irregularities in the orientation and length of the posterior ridges, closely resemble the others. Central ridges on the lateral line scales are shorter and tend to diverge from the center of the impression of the canal. The lateral line canal shows only as the impression of a continuous canal 0.7 mm. in diameter. Preservation is poorest in scales along the line of the neural and haemal arches; therefore lateral line scales are rarely preserved. Isolated scales are of two types: those on which the posterior ridges converge sharply and form the gothic arch configuration mentioned by Hibbard (1933:282), and those which do not. Both types of scales can be present on one fish, as shown by specimen no. 788. This is not apparent on nos. 786F and 787F; all of the scales on these specimens appear to be much alike. Both Moy-Thomas (1937:385) and Schaeffer (1952:51, 52) have remarked on the variation of the scales on different parts of the same fish. Because the number of ridges and amount of convergence of the ridges is not related to size of the scale, it is concluded that these characters are not of taxonomic significance.

The strong resemblance of the scales of the Garnett specimens to those of *Rhabdoderma elegans* (Newberry) caused Moy-Thomas (1937:399) to add Hibbard's two species to the synonymy of *R. elegans*. But at that time only the scales could be adequately described. If the shape of the scale and the number and pattern of ridges can vary with age, size and shape of the scale, it follows that assignment of isolated scales to a species should not be attempted. Assignment to genus should be made only with caution.

Discussion.—The relationship of *Synaptotylus* to other coelacanths is obscure at present. The knoblike antotic processes on the basisphenoid are unlike those of any other known coelacanth. The palatoquadrate complex is shaped like that of *Rhabdoderma elegans* but consists of fewer bones, probably because of fusion. The scales resemble those of *Rhabdoderma*. With regard to general shape of fin girdles, the pectoral girdle resembles that of *Eusthenopteron* more than that of *Rhabdoderma*, but the cleithrum is more nearly like the cleithrum of *Rhabdoderma*. The pelvic girdle appears to be midway between those of *Rhabdoderma* and *Coelacanthus* in general appearance. Regarding the basal plates of the remaining fins, those of *Synaptotylus* appear to resemble basal plates of both *Rhabdoderma* and *Coelacanthus*. Considering the structure of the sphenethmoid region of the braincase, *Synaptotylus* is probably

more closely related to *Rhabdoderma* than to other known coelacanth genera.

COMMENTS ON CLASSIFICATIONS

Classification of Carboniferous coelacanths has been difficult, partly because the remains are commonly fragmentary, and significant changes in anatomy did not become apparent in early studies. In general, coelacanths have been remarkably stable in most characters, and it has been difficult to divide the group into families. As Schaeffer (1952:56) pointed out, definition of coelacanth genera and species has previously been made on nonmeristic characters, and the range of variation within a species has received little attention. For example, Reis (1888:71) established the genus *Rhabdoderma,* using the strong striation of the scales, gular plates and posterior mandible as the main characters of this Carboniferous genus. Moy-Thomas (1937:399-411) referred all Carboniferous species to *Rhabdoderma*, redescribed the genus and compared it to *Coelacanthus,* the Permian genus. He cited as specific characters the ornamentation of the angulars, operculars and gular plates (Moy-Thomas, 1935:39; 1937:385). Individual variation in some species has rendered ornamentation a poor criterion. This variation is apparent in *Synaptotylus newelli* (Hibbard), some specimens having little or no ornamentation; others having much more. The number of ridges and pattern of ridges on the scales also varies. Schaeffer (1952:56) has found this to be true of *Diplurus* also. Moy-Thomas (1935:40; 1937:385) realized that the type of scale is a poor criterion for specific differentiation. In the search for features useful in distinguishing genera of coelacanths, Schaeffer and Gregory (1961:3, 7) found the structure of the basisphenoid to be distinctive in known genera, and thought it had taxonomic significance at this level. Higher categories should have as their basis characters that display evolutionary sequences. A recent classification (Berg, 1940), followed in this paper, reflects two evolutionary trends in endocranial structure of coelacanths: reduction of endocranial ossification and loss of the basipterygoid processes. Because there has been little change in other structures in coelacanths, Berg's classification is the most useful. Berg (1940:390) includes *Rhabdoderma* in the suborder Diplocercidoidei because of the presence of the basipterygoid processes, and in the single family, Diplocercidae, but remarks that because of the reduced amount of endocranial ossification the Car-

boniferous Diplocercidae "probably constitute a distinct family."
In considering this concept of classification, the subfamilies Diplo-
cercinae and Rhabdodermatinae of the family Diplocercidae are
proposed above.   The subfamily Rhabdodermatinae includes at
present *Rhabdoderma* and *Synaptotylus*.   The principal characters
of the subfamily Rhabdodermatinae, named for the first known
genus, are the retention of the basipterygoid processes and the
reduction of endocranial ossification.   Application of this classifica-
tion based upon endocranial structure would probably change
existing groupings of species of Carboniferous coelacanths; the
entire complex of Carboniferous genera should be redescribed and
redefined.   It will be necessary to consider endocranial structure
in any future classification.

The greater part of the evolution previously mentioned appears
to have been accomplished during the Carboniferous; thereafter
coelacanth structure became stabilized.   The trend progressed from
Devonian coelacanths which had two large unpaired bones in the
endocranium, and both antotic and basipterygoid processes on the
basisphenoid, to Carboniferous fishes in which ossification was
reduced to a number of paired and unpaired bones embedded in
cartilage, and retaining both processes, and then post-Carboniferous
kinds with reduced ossification and no basipterygoid processes.
The Pennsylvanian was evidently the time of greatest change for
the coelacanths, and they have not changed significantly since, in
spite of the fact that since the Jurassic they have shifted their en-
vironment from shallow, fresh water to moderate depth in the sea
(Schaeffer, 1953:fig. 1).   The changes in endocranial structure
appear to be significant, and are perhaps related to higher efficiency
of the mouth parts in catching and swallowing prey (see p. 482).

ENVIRONMENT

The coelacanth fishes from the Rock Lake shale are part of the
varied fauna collected from Garnett.   Peabody (1952:38) listed
many elements of the fauna and flora, and concluded that the de-
posits are of lagoonal origin.   In addition to numerous inverte-
brates (including microfossils) and arthropods, a number of verte-
brates other than coelacanths have been found.   These include at
least one kind of shark, *Hesperoherpeton garnettense* Peabody, one
or more kinds of undescribed labyrinthodonts and the reptiles
Petrolacosaurus kansensis Lane, *Edaphosaurus ecordi* Peabody, and
Clepsydrops (undescribed species).   This is indeed a rich vertebrate

fauna, and the earliest known reptilian fauna. Much of the rock contains plant remains. The flora that has been identified is adapted to growing in a well-drained soil; although it contains some elements considered characteristic of the Permian, it is of Pennsylvanian age (Moore *et al.*, 1936). Peabody (1952:38-39) discusses the features of these lagoonal sediments. Much of the fauna and flora suggests continental origin, but the many marine invertebrates at some horizons indicate that at least some of the sediments were of marine origin.

Little can be said about the actual environment of the living fishes of the genus *Synaptotylus*. Remains of these fishes occur in layers containing marine invertebrates, as well as in those containing plant remains and vertebrate skeletal parts, and in those nearly completely composed of dark carbonaceous material. Most of the remains are fragmentary and consist of isolated bones, isolated scales, and dissociated skulls; only one specimen and half of another are nearly complete. Many published statements on *Rhabdoderma*, a related genus, indicate both marine and fresh-water environments. Wehrli (1931:115) regarded *Rhabdoderma elegans* (Newberry) as a euryhaline species, and cited its occurrence with both marine and fresh-water fossils. Aldinger (1931:199) also found this to be the case with other species, and Fiege (1951:17) quotes others as giving the same information. Keller (1934:913) thought that few Carboniferous fishes were exclusively marine, and stated that the majority of them became adapted to fresh water during the late Carboniferous. Later, Schaeffer (1953:175) stated that all Carboniferous and Permian coelacanths were fresh-water fishes, and that many were from swamp deposits. If Keller is correct, then members of the genus *Synaptotylus* may have inhabited the lagoon, the adjacent sea, or the streams draining into the lagoon. Perhaps these fishes swam upstream, as modern salmon and tarpon do, although there is no direct evidence for this. Possibly they lived in the lagoon at times of scant rainfall and little runoff, when the salinity of lagoon water approached normal marine values or the fishes may have lived in the streams, and after death were washed into the lagoon. As numerous remains of land plants and animals were washed in, perhaps this best accounts for the presence of the fish in nearly all layers of the deposits, not only the marine strata.

SUMMARY

A new genus of Pennsylvanian coelacanths, *Synaptotylus*, is described and a previously named species, *Coelacanthus newelli* Hibbard, 1933 (*C. arcuatus* Hibbard, 1933, is a junior synonym), is referred to this genus. All specimens of *Synaptotylus newelli* (Hibbard) were collected from the Rock Lake shale member of the Stanton formation, Lansing group, Missouri series, six miles northwest of Garnett, Anderson County, Kansas. *Synaptotylus* is distinguished from all other coelacanths by a basisphenoid having large, knoblike antotic processes each connected by a low ridge to a small basipterygoid process. *Synaptotylus* is most closely related to *Rhabdoderma*, but is intermediate between *Rhabdoderma* and *Coelacanthus* in shape of the fin girdles and basal plates. Two new subfamilies, Diplocercinae and Rhabdodermatinae, of the family Diplocercidae, are proposed. *Synaptotylus* and *Rhabdoderma* are included in the subfamily Rhabdodermatinae, because both exhibit reduced ossification in the endocranium and retain basipterygoid processes.

Loss of the basipterygoid processes in post-Carboniferous coelacanths may reflect the development of a more efficient feeding mechanism, by allowing the palatoquadrate complex and mandible to swing farther laterally and expand the oral cavity.

Synaptotylus newelli (Hibbard) may have occupied either the sea or fresh water; these fishes occur in lagoonal deposits with reptiles and amphibians, arthropods, marine invertebrates and remains of land plants.

Because scale patterns on *Synaptotylus* and *Rhabdoderma* are so nearly similar and vary with size of the scale and its location on the fish, it is recommended that isolated scales not be assigned to a species, and to a genus only with great caution.

LITERATURE CITED

Aldinger, H.
  1931. Ueber karbonische Fische aus Westfälen. Paleont. Zeit., 13:186-201.

Berg, L. S.
  1940. Classification of fishes, both Recent and fossil. Moscow and Leningrad, 1940 (J. W. Edwards, Ann Arbor, Michigan, 1947, offset reproduction, pp. 1-345, 197 figs., plus English translation of text, pp. 346-517, 1947.

Fiege, K.
  1951. Eine Fisch-Schwimmspur aus dem Culm bei Waldeck. Neues Jahrb. Geol. and Paläont. Jahrgang 1951:9-31.

Hibbard, C. W.
  1933. Two new species of *Coelacanthus* from the middle Pennsylvanian of Anderson County, Kansas. Kansas Univ. Sci. Bull., 21:279-287.

Keller, G.
  1934. Fischreste aus dem oberkarbon des Ruhrgebiets. Gluckauf, 70: 913-917.

Moore, R. C., Elias, M. K., and Newell, N. D.
  1936. A "Permian" flora from the Pennsylvanian rocks of Kansas. Jour. Geol., 44:1-31.

Moy-Thomas, J. A.
  1935. A synopsis of the coelacanth fishes of the Yorkshire Coal Measures. Ann. Mag. Nat. Hist., 15 (ser. 10): 37-46.
  1937. The Carboniferous coelacanth fishes of Great Britain and Ireland. Proc. Zool. Soc. London, 107 (B): 383-415.

Peabody, F. E.
  1952. *Petrolacosaurus kansensis* Lane, a Pennsylvanian reptile from Kansas. Kansas Univ. Paleont. Contrib., 1:1-41.

Reis, O. M.
  1888. Die Coelacanthinen mit besonderen Berücksichtigung der im Weissen Jura Bayerns verkommenden Arten. Palaeontographica, 35: 1-96.

Schaeffer, B.
  1952. The Triassic coelacanth fish *Diplurus*, with observations on the evolution of the Coelacanthini. Bull. Amer. Mus. Nat. Hist., 99: art. 2, 29-78.
  1953. *Latimeria* and the history of the coelacanth fishes. New York Acad. Sci. Trans., (2) 15:170-178.

Schaeffer, B., and Gregory, J. T.
  1961. Coelacanth fishes from the continental Triassic of the western United States. Amer. Mus. Novitates, 2036:1-18.

Schaeffer, B., and Rosen, D. E.
  1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. Am. Zool., 1:187-204.

Smith, J. L. B.
  1939. A living coelacanthid fish from South Africa. Trans. Roy. Soc. South Africa, 28:1-106.

Stensiö, E. A.
  1921. Triassic fishes from Spitzbergen. Part I. Vienna, Adolf Holzhausen: 1-307.
  1932. Triassic fishes from East Greenland. Meddel. om Grønland, 38: 1-305.

TCHERNAVIN, V. V.
  1948. On the mechanical working of the head of bony fishes. Proc. Zool.
         Soc. London, 118:129-143.
WEHRLI, H.
  1931. Die Fauna der Westfälischen Stufen A und B der Bochumer Mulde
         zwischen Dortmund und Kamen (Westfalen). Palaeontographica,
         74:93-134.